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Abstract

Classification of species sensitivity for biomonitoring has been approached under two different frameworks, using either empirical data or expert opinion. Two tools for fine sediment biomonitoring in the United Kingdom tend towards these contrasting approaches. The Proportion of Sediment-sensitive Invertebrates (PSI) index was developed using expert judgement. Empirical weightings were subsequently added at genus or species (EPSI) and mixed ($EPSI_{mixed}$) taxonomic levels but scores remain constrained by the original categories. In contrast, the Combined Fine Sediment Index (CoFSI), composed of separate taxon scores along organic matter (OFSI) and total fine sediment (ToFSI) gradients, was developed using a purely empirical approach. We tested the mechanistic bases for these indices by relating taxon scores to species traits. We compared the results with those for the well-established Walley Hawkes Paisley Trigg (WHPT) index of organic pollution. After controlling for varying sample sizes, WHPT could be better predicted by a linear combination of all available traits (mean R^2=0.92) than any of the fine sediment indices (0.68<mean R^2<0.76). When only traits expected to respond to fine sediment were offered as independent variables, the goodness-of-fit was substantially reduced for all fine sediment indices (0.27<mean R^2<0.46). Our findings demonstrate the lack of integration between the literature on macroinvertebrate responses to fine sediment, the available trait data, and taxon scores. Refinement of the trait database is recommended to build on the valuable work done to date. Since the United Kingdom has taken the lead in embedding fine sediment into routine

biomonitoring programmes, these findings have important international implications.

Introduction

Classifications of sensitive or tolerant species have long been used to monitor the aquatic environment (e.g. Kolkwitz & Marsson, 1909). Worldwide, this activity has been undertaken within two very different frameworks: on the one hand using an objective, data-driven approach to locate taxa along a stress gradient (e.g. Whittier & Hughes, 1998; Pirhalla, 2004; Murphy et al., 2015), and on the other hand through relying on expert judgement to assign scores to taxa based on existing information about their sensitivity or tolerance to the stressor of interest (e.g. Armitage et al., 1983; Barbour et al., 1999; Extence et al., 2011). A current debate about biomonitoring for fine sediment in the United Kingdom rests on the contrast between these two approaches. Resolving this debate has important consequences for the practice of biomonitoring throughout Europe and other regions of the world, where pressure-specific indices for fine sediment have yet to be widely developed.

Fine sediment is a particularly pervasive stressor of river ecosystems, with adverse impacts arising from its accumulation within substrata (*i.e.* colmation) and its transportation in suspension (Wood & Armitage, 1997; Bilotta & Brazier, 2008; Jones et al., 2012). Negative impacts are evident at all trophic levels, from primary producers (Van Nieuwenhuyse and LaPerriere, 1986; Klco, 2008) to top predators relying on visual searching behaviour (Gardner, 1981; Berkman and Rabeni, 1987). This is of particular concern in sport fish spawning gravels which are directly affected by the reduction in suitable spawning habitat, smothering of redds and reduced overwintering and fry emergence, in addition to indirect

67 impacts related to prey abundance (Sear et al., 1993; Kemp et al., 2011; Relyea et
68 al., 2012). It is now a primary research area for many freshwater ecology and
69 environmental engineering groups around the world. In Europe, this is partly a
70 result of the focus brought by the implementation of the Water Framework
71 Directive (WFD), leading to the realisation that fine sediment is an important and
72 widespread cause of ecological deterioration linked to drivers as diverse as
73 agriculture, urbanisation, flood management and flow regulation (Collins &
74 Anthony, 2008; Taylor & Owens, 2009; Acreman & Ferguson, 2010).
75
76 Authorities in the United Kingdom use a macroinvertebrate community index
77 known as Walley Hawkes Paisley Trigg (WHPT) for WFD status classification.
78 WHPT scores taxa based on their occurrence (presence-absence) or assigns a log
79 abundance-weighted score in one of four categories (1-9; 10-99; 100-999; and
80 >999 individuals). WHPT evolved from the Biological Monitoring Working Party
81 (BMWP) method, in which taxa were attributed organic pollution sensitivity
82 scores based on expert judgement (Armitage et al., 1983). The index has been
83 refined since the inception of BMWP, most recently by using data-driven
84 optimisation (Paisley et al., 2014). WHPT is among the most well developed
85 biomonitoring tools in the world. This is evidenced by its long history of
86 optimisation and the adoption of the method in many parts of the world (e.g.
87 Diaz et al., 2004; Herman & Nejadhashemi, 2015). This history demonstrates the
88 pioneering role that the United Kingdom has played in index development,
89 something which it continues to do in the context of fine sediment
90 biomonitoring.
91

92 Whilst WHPT is a central pillar of WFD classification in the UK, diagnosing the
93 cause of ecological degradation and classifying ecological status more accurately
94 requires the use of a range of pressure-specific indicators. In the United Kingdom
95 there are currently two such groups of indices for fine sediment: those related to
96 the Proportion of Sediment-sensitive Invertebrates (PSI) index; and those
97 comprising the Combined Fine Sediment Index (CoFSI). In the development of
98 the PSI scoring system taxa were subjectively assigned to one of four Fine
99 Sediment Sensitivity Rating (FSSR) categories: (A) highly sensitive; (B) sensitive;
100 (C) tolerant; and (D) highly tolerant, based on a review of existing empirical
101 information primarily published in ecological monographs and identification
102 keys (Extence et al., 2011). Weightings for each taxon were later computed using
103 extensive monitoring data by Turley et al. (2015) at the genus and species levels
104 (EPSI), and by Turley et al. (2016) at mixed taxonomic levels ($EPSI_{mixed}$), to
105 enhance the empirical basis for PSI. However, the resulting scores (%) still
106 remain constrained by the original FSSR categories.
107
108 CoFSI was developed more recently using a highly statistical approach (Murphy
109 et al., 2015) whereby a number of environmental gradients, determined from
110 extensive fieldwork, were reduced to two axes using partial Canonical
111 Correspondence Analysis (pCCA). The resulting axes, describing gradients of
112 total fine sediment (Total Fine Sediment Index; ToFSI) and organic matter
113 (Organic Fine Sediment Index; OFSI), were then used to derive species scores
114 based on their projected position along each axis, followed by calculation of a
115 combined score at the community level. Thus the procedure was entirely data-
116 driven, leaving no room for the use of extensive prior knowledge from the

117 literature. As a result of differences in their development, the two tools (EPSI and
118 CoFSI) often assign different scores to the same taxa (e.g. Figure 1).
119
120 Direct comparison of the two sets of indices (PSI- and CoFSI- related) is
121 challenging due to differences in the methods used in their development. The
122 original PSI index was calibrated using visual estimates of surface fine sediment
123 cover (Turley et al., 2014). In contrast, CoFSI was calibrated using the sediment
124 resuspension technique (Duerdoth et al., 2015). We avoid the pitfalls of direct
125 comparisons by focusing on the mechanistic basis for fine sediment
126 biomonitoring using data on species traits.
127
128 Trait-based approaches to freshwater biomonitoring have been growing in
129 popularity (Menezes et al., 2010; Statzner & Bĕche, 2010). This is due to
130 methodological advances (Cornwell et al., 2006; Villéger et al., 2008; Laliberte &
131 Legendre, 2010; Schleuter et al., 2010) and the availability of fuzzy coded data
132 describing species traits (e.g. Tachet et al., 2010). However, attempts to develop
133 robust predictive tools based on trait-environment relationships have been met
134 with frustration (Verberk et al., 2013), and many trait-based approaches to the
135 development of biomonitoring tools are informed by expert interpretation of
136 primary literature rather than any published trait databases (e.g. Extence et al.,
137 2011).
138
139 We assessed the degree to which taxon scores under EPSI and CoFSI are related
140 to species traits drawn from the widely used trait database of Tachet et al.
141 (2010). We considered linear models for each index using a series of traits

describing life-history, morphology, physiology and behaviour as independent variables. As the most well-developed biomonitoring index, we compare the results with models for WHPT.

Methods

Index scores and trait values

Taxon scores for WHPT (UKTAG, 2014), empirical weightings for EPSI (Turley et al., 2015) and $EPSI_{mixed}$ (Turley et al., 2016) and taxon scores under CoFSI (Murphy et al., 2015) were taken from their respective sources. We considered models for OFSI and ToFSI scores as well as the combined CoFSI score for each individual scoring taxon (see equation 2 in Murphy et al., 2015). For WHPT we explored separate models predicting scores for presence-absence, the mean of abundance-weighted scores for each scoring taxon, and the high abundance score for each scoring taxon. The results of these alternative models were very similar (Figure A1). We therefore focused on WHPT presence-absence scores for simplicity in the remainder of our modelling. Prior to the modelling all index scores were centred and standardised in order to aid interpretation of model coefficients.

Where possible, index scores were matched with fuzzy coded trait values from Tachet et al. (2010) as alternative databases were largely incomplete (e.g. Schmidt-Kloiber & Hering, 2015) for 'true' traits, *i.e.* not those reflecting ecological preferences (Statzner & Bĕche, 2010; Verberk et al., 2013). In

167 instances where index scores were available at a coarser taxonomic level than
168 traits, fuzzy values were averaged across genera or species. This resulted in a
169 total number of taxa for which matched trait data were available of 106 (WHPT),
170 421 (EPSI), 348 ($EPSI_{mix}$) and 95 (CoFSI, OFSI, ToFSI) for the respective indices.
171 Taxonomic resolution for WHPT was family level, whereas fine sediment indices
172 were generally at species level (see supplementary material).
173
174 The complete trait dataset encompassed 63 trait modalities (hereafter referred
175 to as 'traits' for brevity) in 11 trait categories (Table A1). After compiling lists of
176 scoring taxa and their traits separately for each index, individual trait modalities
177 were centred and standardised within a trait category to give equal weights
178 across all trait categories. As some traits describing type of food and feeding
179 mode were moderately correlated ($0.6<r<0.75$) we considered removing the
180 correlated food types. However, since variance inflation factors (VIFs) were low
181 (<2), it was decided to keep the full set of food types. Finally, a subset of traits
182 that are purported to be instrumental in conferring tolerance or sensitivity to
183 fine sediment was selected based on a review of the literature (Table A1).
184
185 *Modelling approach*
186
187 A multiple linear regression approach was taken to predict scores under each
188 index using a combination of traits. All analyses were performed in R 3.2.3 (R
189 Core Team, 2015). Goodness-of-fit was assessed for several sets of models. The
190 first three sets ('global' models) included all taxa for which scores were available
191 under the respective indices: (i) the global 'all traits' model using all 63 traits; (ii)

192 the global model 'pruned' using stepwise selection in both directions (*stepAIC*
193 function, MASS package; Venables & Ripley, 2002); and (iii) the global 'literature'
194 model using only the subset of 35 traits drawn from the literature (Table A1).
195 For each index, nested global models were compared using the *anova* function.
196 We did not explore literature-based models for WHPT.
197
198 Due to the bias introduced by inequalities in the number of scoring taxa for each
199 index, we generated another set of model results by taking 1000 random
200 samples of 90 taxa: (v) the 'all traits minimum' model; (vi) the 'pruned minimum'
201 model; and (vii) the 'literature minimum' model. Finally, to assess the sensitivity
202 of WHPT models to trait averaging at the family level, modelling for the all traits
203 minimum and pruned minimum scenarios was repeated for 100 random
204 samples of sub-family level (genus or species) traits within WHPT families, with
205 50 samples of 90 taxa for each set of sub-family level traits (5000 samples in
206 total). All sampling was performed without replacement using the *sample*
207 function. In all cases we used R^2 as a measure of goodness-of-fit.
208
209 **Results**
210
211 The global 'all traits' and 'pruned' models for WHPT had a higher goodness-of-fit
212 than equivalent models for the fine sediment indices (Table 1). In turn, the
213 goodness-of-fit for global EPSI and $EPSI_{mixed}$ models was substantially lower than
214 for CoFSI, OFSI and ToFSI. However, these results do not allow direct comparison
215 between indices due to variations in the number of scoring taxa, which affects
216 statistical power (Cohen, 1992). When offering only the literature-based traits as

217 explanatory variables the performance of global models for the fine sediment
218 indices was greatly reduced. The global 'all traits' model did not improve
219 predictions significantly ($p>0.05$), except in the case of the EPSI literature model
220 ($p<0.02$), *i.e.* in most cases the fit of more parsimonious 'pruned' models was not
221 significantly different to that of the more complex 'all traits' models (Table 1).
222 Thus, we focus primarily on the global 'pruned' models to assess trait-index
223 relationships (Figure 2).
224
225 The WHPT global 'pruned' model retained significant explanatory variables in
226 several trait categories, including aquatic stages, respiration and feeding modes,
227 diet and voltinism (Figure 2a). The global 'pruned' models for EPSI and $EPSI_{mixed}$
228 retained similar sets of traits (Figure 2b-c). The traits most strongly driving
229 species sensitivity under these indices were 'AttachedTemp', 'Shredder', and
230 'Scraper'. Those most strongly indicating tolerance were 'Adult' and 'Flier',
231 although the latter was not significant ($p>0.05$). The CoFSI global 'pruned' model
232 retained a different set of coefficients, including several diet-, feeding mode-,
233 locomotion- and resistance- related traits (Figure 2d). The OFSI and ToFSI global
234 'pruned' models shared significant coefficients for traits describing voltinism,
235 ovoviviparity, tegumental respiration and feeding modes, yet the sign of
236 coefficients for these traits was opposite under each index (Figure 2e-f). In
237 general, the OFSI model was more strongly related to traits describing
238 respiration modes.
239
240 No traits were consistently associated with tolerance under all fine sediment
241 indices. Only 'Shredder' was consistently associated with sensitivity. CoFSI and

242 the PSI-related indices also shared strong and significant positive coefficients for
243 'AttachedTemp' and 'Crawler'. 'Scraper' indicated sensitivity in all cases except
244 ToFSI. There were opposite signs in trait-stressor relationships between the two
245 groups of fine sediment indices for 'Small', 'AerialActive', 'Ovoviviparity',
246 'Cocoons', 'Perren' (life cycle duration >1 year), 'OpenWaterSwimmer', 'Parasite',
247 'Predator', 'DeadAnimal' and 'DiapauseDormancy'.
248
249 With regards to the global 'literature' models, several literature-based traits
250 were significant predictors of EPSI and $EPSI_{mixed}$ weightings ($p<0.05$), whereas
251 relatively few of the traits purported to be important in determining sensitivity
252 or tolerance to fine sediment in the literature were significant predictors of OFSI
253 or ToFSI scores (Table 2). There were a number of inconsistencies in the sign of
254 relationships expected from the literature review and those observed in the
255 global literature models (Table 2).
256
257 Figure 3 shows goodness-of-fit for the 'minimum' models. These results are
258 directly comparable between indices as they are not biased by variations in the
259 number of scoring taxa. The minimum 'all traits' (Figure 3a) and 'pruned' (Figure
260 3b) WHPT models, which were robust to trait averaging at the family level,
261 performed better than the fine sediment indices. When only traits drawn from
262 the literature review were included as explanatory variables, the goodness-of-fit
263 for all fine sediment indices was again greatly reduced (Figure 3c). After
264 controlling for the number of scoring taxa, the fit of models for alternative fine
265 sediment indices was similar.
266

Discussion

A large body of literature is forming around the response of macroinvertebrates to fine sediment (see reviews by Wood & Armitage, 1997; Bilotta & Brazier, 2008; Jones et al., 2012). This includes several studies focusing explicitly on species traits (Gayraud & Phillipe, 2001; Wagenhoff et al., 2012; Buendia et al., 2013; Descloux et al., 2014), which have been employed to good effect in a range of other applications, including flow intermittence (Datry et al., 2014), insecticides (Rico & Van den Brink, 2015) and multiple agricultural stressors (Lange et al., 2014). In Europe, these traits are typically drawn from the database of Tachet et al. (2010), which is limited to 63 true traits in 11 categories.

The aforementioned literature has the potential to contribute towards progress in biomonitoring. However, in the case of fine sediment, our findings demonstrate the need for more integration of the available trait data, the a priori expectations from the literature, and the scores assigned to taxa under currently available pressure-specific indices. This is evidenced by the relatively poor fit of trait-based models for fine sediment indices, especially when only traits drawn from the literature review were entered as explanatory variables. It is further reinforced by the differences in significant traits retained in models for alternative fine sediment indices.

Taxon scores under WHPT were strongly related to traits conferring tolerance or sensitivity to organic pollution (Tomanova et al., 2008; Archaimbault et al., 2010; Feio & Dolédec, 2012). WHPT scores were negatively related to taxa with

292 tegumental respiration and aquatic lives strongly skewed towards adult life-
293 stages (*e.g.* Acroloxidae, Dugesiidae) and positively to univoltine shredders (*e.g.*
294 Lepidostomatidae) and taxa with a range of aquatic life stages, including eggs
295 (*e.g.* Gyrinidae). In contrast, few traits with strong and significant coefficients in
296 the models for fine sediment indices could be related to the extant literature on
297 trait-fine sediment relationships. Some traits had coefficients with conflicting
298 signs between the two sets of indices. This is surprising given that both were
299 designed for biomonitoring of the same stressor. Before discussing these
300 differences in detail, it is worth noting two important nuances of the findings
301 reported.
302
303 Firstly, CoFSI, OFSI and ToFSI had a substantially higher R^2 than EPSI and
304 $EPSI_{mixed}$ for the global models (Table 1) but marginally lower for the 'minimum'
305 models (Figure 3). The CoFSI-related indices also had fewer significant variables
306 than the PSI-related indices in the global literature-based models (Table 2),
307 despite a better fit. This is because the much lower number of scoring taxa under
308 CoFSI meant that the resulting models had a higher type II error rate (Cohen,
309 1992). Secondly, some traits with significant coefficients in the global pruned
310 models (Figure 2) did not have significant coefficients in the global literature
311 models (Table 2). This is because the significance of each coefficient is assessed
312 in the presence of all other independent variables, and the pruned models
313 retained traits that were not included in the literature models.
314
315 Only a single trait ('Shredder') was consistently associated with sensitivity
316 across all five fine sediment indices (PSI- and CoFSI- related). Both Buendia et al.

317 (2013) and Descloux et al. (2014) also found shredders to be relatively sensitive.
318 The mechanism for this may be the burial of leaf litter and/or a reduction in its
319 nutritional quality through inhibition of fungal growth (Febra, 2013). This is
320 similar to the mechanism posited for the sensitivity of scrapers (Brookes, 1986;
321 Suren, 2005; Kent & Stelzer, 2008; Jones et al., 2012; Relyea et al., 2012), which
322 were also consistently associated with sensitivity in all pruned models except
323 ToFSI. The next strongest association with sensitivity across the majority of fine
324 sediment indices was for temporarily attached organisms. However, Descloux et
325 al. (2014) reported this trait to be indicative of tolerance across three rivers in
326 Germany. Buendia et al. (2013) found that temporarily attached taxa were
327 present in sediment-laden tributaries of the River Isábena in the Central
328 Pyrenees but reported no significant correlation. Finally, crawlers were also
329 associated with sensitivity under CoFSI, EPSI and $EPSI_{mixed}$. This is consistent
330 with Buendia et al. (2013), who reported a significant negative correlation
331 between the prevalence of crawling as a trait and the rank of sites increasingly
332 affected by fine sediment deposition. On the other hand, Descloux et al. (2014)
333 found a consistently significant positive correlation between the relative
334 occurrence of crawlers and colmation.
335
336 Several further traits were inconsistently associated with sensitivity or
337 tolerance, having coefficients with opposite signs under the various indices.
338 These included small taxa (2.5-5 mm), aerial (active) dispersers, ovoviviparous
339 reproducers, parasites, predators, perennial organisms and those with strong
340 resistance traits for cocoons and diapause or dormancy. Such equivocal results
341 suggest that there is a problem in the trait-literature-biomonitoring nexus. The

problem may lie with the literature, with the way that traits are described, or with the development of the biotic indices. It is most likely to be a combination of these factors. This likelihood is further reinforced by the fact that our models lacked significant coefficients for a range of other traits purported to important in fine sediment response in the literature (Table A1).

Body size

Small-bodied taxa (<5 mm) are expected to be strongly sensitive to fine sediment due to smothering and restricted dispersal in reduced pore space (Gayraud & Phillipe, 2001; Wood et al., 2001; Wagenhoff et al., 2012; Descloux et al., 2014). However, body size did not feature strongly in our models.

Life cycle duration and voltinism

Based on the literature, we expected perennial and uni- or semi-voltine taxa to be sensitive and ephemeral and multivoltine taxa to be relatively tolerant (Larsen et al., 2011; Buendia et al., 2013). Semivoltine and perennial taxa were tolerant according to the pruned models for EPSI, $EPSI_{mixed}$ and CoFSI but voltinism traits were associated with either sensitivity (OFSI) or tolerance (ToFSI) under the CoFSI sub-indices, indicating that the combination of axes describing organic matter and total fine sediment under CoFSI may cancel out distinct mechanisms of the fine sediment impact. Only ToFSI had a significant coefficient for any life-history trait (semivoltine, tolerant) among the literature-based models. Ephemeral or multivoltine taxa were not found to be tolerant

367 under any of our models, with the exception of ToFSI. On the contrary, these
368 traits were strongly linked with sensitivity under OFSI.
369
370 *Aquatic life-stages*
371
372 Life-stage can affect an organism's ability to avoid burial and excavate itself,
373 although there is much variability between taxa for a given life-stage (Wood et
374 al., 2001; 2005). Certainly, immotile eggs are expected to be negatively impacted
375 by fine sediment (Jones et al., 2012) and this was supported in literature-based
376 models for EPSI and $EPSI_{mixed}$. Models for CoFSI and ToFSI indicated that taxa
377 with strong larval life-stages are tolerant, whilst models for EPSI, $EPSI_{mixed}$ and
378 ToFSI indicated the same for adult life-stages. However, the picture is far from
379 clear because of the way fuzzy coded traits are organised, which is a problem
380 when focusing on life-stage. For example, a taxon which is aquatic as an egg,
381 larva, pupa and adult would receive equal fuzzy codes across all four trait
382 modalities. The results for life-stages, therefore, must be seen as representing
383 the level of aquatic specialism rather than the sensitivity of a given life-stage *per*
384 *se*. Advances in trait-based biomonitoring would benefit from ontogenetic
385 information (Statzner & Bĕche, 2010).
386
387 *Reproduction and resistance*
388
389 There is little information in the literature as to how reproduction and resistance
390 traits are expected to respond to fine sediment. Descloux et al. (2014) found that
391 ovoviviparity was less prevalent at impacted sites and that cocoons and asexual

392 reproduction varied significantly across the gradient of colmation, although the
393 sign of these relationships was not consistent among three rivers. In the pruned
394 models there were significant coefficients for 'cocoons' (EPSI, tolerant),
395 'DiapauseDormancy' (ToFSI, sensitive) and asexual reporoduction ($EPSI_{mixed}$,
396 sensitive). The EPSI and OFSI pruned models indicated that ovoviviparous taxa
397 are tolerant, whereas the equivalent ToFSI model indicated sensitivity for the
398 same trait, again suggesting that the combination of organic matter and total fine
399 sediment gradients under CoFSI may obscure discrete processes.
400
401 *Diet and feeding mode*
402
403 The literature contains a relative richness of information upon which to base a
404 priori expectations for traits describing diet and feeding mode. The majority of
405 this information points to sensitivity of shredders and scrapers due to burial and
406 dilution of food resources and reductions in nutritional quality (Brookes, 1986;
407 Suren, 2005; Kent & Stelzer, 2008; Relyea et al., 2012; Febra, 2013), and of filter-
408 feeders due to the clogging of feeding apparatus (Kurtak, 1978; Lemly, 1982;
409 Edington & Hildrew, 1995; Strand & Merrit, 1997) as well as a decline in
410 nutritional quality (Nuttall & Bielby, 1973), although the empirical evidence
411 from recent work focusing explicitly on traits is often equivocal on this (Buendia
412 et al., 2013; Descloux et al., 2014). As discussed above, the sensitivity of
413 shredders and scrapers was supported by our findings, but no other consistent
414 relationships between taxon scores and diets or feeding modes were evident.
415
416 *Respiration*

Of the respiration traits available, we expected to find significant associations between taxon scores and tegumental and gill respiration modes. Descloux et al. (2014) reported a significant reduction in tegumental respiration and a significant increase in gill respiration across a gradient of colmation. Buendia et al. (2013) also found that gills conferred tolerance. However, this is counterintuitive as organisms with tegumental respiration are typically associated with tolerance to oxygen depletion, which is characteristic of fine sediment stress (Tomanova et al., 2008; Larsen et al., 2011; Von Bertrab et al., 2013). On the other hand, organisms with gills have previously been reported as sensitive (Townsend et al., 2008; Larsen et al., 2011) due to abrasion and clogging of the breathing apparatus (Lemly, 1982; Culp et al., 1986; Jones et al., 2012). Gills did not feature strongly in any of our models but tegumental respiration was a significant indicator of tolerance in the literature-based model for EPSI and the pruned model for OFSI. The latter also included spiracle respiration. This reflects the closer association of OFSI with the content of organic matter (Murphy et al., 2015), which is linked to the important role of oxygen availability and sediment quality (Von Bertrab et al., 2013). Tegumental respiration was indicated as sensitive in the ToFSI pruned model, again suggesting that the invertebrate response to organic matter and total fine sediment may be discrete.

Locomotion and relation to the substrate

441 Given that locomotion traits describe an organism's habitat use, they should be
442 strongly linked to fine sediment. Indeed, both Buendia et al. (2013) and Descloux
443 et al. (2014) consistently found that open water swimmers, burrowers and
444 interstitial organisms were sensitive. Interstitial organisms in particular are
445 expected to be susceptible to smothering and restrictions to movement with
446 increasing fine sediment (Wood et al., 2005; Jones et al., 2012), yet this was only
447 supported by pruned and literature-based models for CoFSI and ToFSI. Crawlers
448 are not identified in the literature as either sensitive or tolerant, but pruned
449 models for EPSI, EPSImixed and CoFSI strongly indicated sensitivity for this trait.
450 Evidence for other locomotion traits in our results and in the wider literature is
451 equivocal.
452
453 *Refining traits for fine sediment biomonitoring*
454
455 Both of our main findings - that (i) the performance of trait-based models for fine
456 sediment indices was inferior to those for WHPT and (ii) that traits retained in
457 the models were inconsistent and difficult to reconcile with the literature - may
458 be partly attributable to the lack of relevant traits in the trait database of Tachet
459 et al. (2010). Our findings suggest the need to build upon the excellent work of
460 Tachet et al. (2010) in the context of fine sediment. We therefore recommend a
461 refined set of traits specifically for fine sediment biomonitoring.
462
463 There is a difference between species that actively forage by swimming in open
464 water (e.g. *Notonecta*) and those that use swimming as an escape strategy but
465 would potentially be impacted by fine sediment deposition (e.g. *Cloeon*), yet both

466 receive fuzzy scores for 'OpenWaterSwimmer' in the trait database. The
467 sensitivity of taxa with fixed eggs (*e.g*. 'IsolatedEggsCemented') depends on what
468 the eggs are fixed to (stones, wood, plants) and where (shallow zone, margin,
469 hyporheic zone). The sensitivity of filter-feeders depends on their ability to
470 excrete excess fines: insect filter feeders (e.g. Simuliidae, Hydropsychidae) are
471 likely to be sensitive whereas lower taxa that able to excrete inert fine matter
472 (e.g. Unionidae, Sphaeriidae) are likely to be tolerant. Crawlers could be
473 sensitive, such as certain Ephemeroptera (Ciborowski et al., 1977; Corkum et al.,
474 1977; cf. Jones et al., 2012) or tolerant, for example Chironomidae and Caenidae,
475 who burrow into fine sediment (Jones et al., 2012). Burrowers could also be
476 sensitive or tolerant depending on what they burrow into. Some taxa burrow
477 into fine sediment (e.g. Caenidae, some Sialidae), others in coarser substrata (e.g.
478 Ephemeridae). The same argument applies to other traits describing relation to
479 substrate. Finally, some gills are easily clogged (e.g. Potamanthidae, *Serratella*),
480 others (e.g. Caenidae) are not (Corbin & Goonan, 2010). Physical adaptation in
481 the latter and behavioural adaptation in others (e.g. *Baetis*) confers tolerance to
482 colmation (Buffagni et al., 2009).
483
484 Thus, we recommend the following refinements to the trait database: (i) split
485 open water swimmers into two categories (active foraging, escape); (ii)
486 consolidate several reproduction traits into fixed versus free eggs and include
487 more information on preferred oviposition sites; (iii) split filter-feeder trait into
488 those able and unable to excrete excess fines; (iv) a split involving anatomical
489 and/or behavioural adaptations allowing gill respiration in highly sedimented
490 environments and (v) combine traits describing locomotion and relation to

491 substrate with information on substrate preference. The latter suggestion risks
492 criticism due to the circular nature of using substrate preference to indicate fine
493 sediment stress. However, we argue that these traits do not make sense in the
494 absence of such information, and without sufficient and relevant data on 'true'
495 biological traits (*e.g.* excavation capacity; Wood et al., 2005) substrate preference
496 is the only alternative.
497
498 **Conclusions**
499
500 Our findings point to a problem in the trait-literature-biomonitoring nexus
501 within the context of fine sediment. This is evidenced by a relatively poor fit of
502 trait-based models for fine sediment indices compared to WHPT, a lack of
503 consistency in the traits indicating sensitivity and tolerance under CoFSI- and
504 PSI- related biomonitoring tools, and equivocality between our results and
505 evidence from the extant literature. We suggest that progress may lie in the
506 refinement of traits for fine sediment applications, building on the valuable
507 compilations of traits previously published.
508
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510
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514
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Figure legends

Figure 1 Comparison of taxon scores under CoFSI and taxon weightings under EPSI for 71 taxa that score under both indices.

Figure 2 Coefficients for 'global pruned' models: WHPT (a); EPSI (b); EPSI mixed (c); CoFSI (d); OFSI (e); and ToFSI (f). Note that positive coefficients denote traits associated with sensitivity under each index.

Figure 3 Goodness-of-fit for 'minimum' models using all traits (a), traits retained after stepwise selection (b) and literature-based traits (c). Symbols indicate means and whiskers show 95% confidence intervals from random sampling.

Figure A1 Coefficients for 'global pruned' models: WHPT presence-absence (a); the mean of abundance-weighted WHPT scores for each scoring taxon (b); and the high abundance WHPT score for each scoring taxon (c).EPSI (c). Note that positive coefficients denote traits associated with sensitivity.

819 **Table 1** Goodness-of-fit and ANOVA results for global models. The test evaluates
820 the null hypothesis that the fit of the global 'all traits' model is no better than the
821 fit of the more parsimonious model ('pruned', 'literature').
822

All traits model	**n**	**Pruned model**			**Literature model**		
		R^2	**F (*df*)**	***p***	**R^2**	**F (*df*)**	***p***
WHPT (R^2=0.90)	106	0.88	0.24 (*26*)	0.99	NA	NA	NA
EPSI (R^2=0.36)	421	0.34	0.32 (*32*)	0.99	0.28	1.73 (*26*)	0.02
$EPSI_{mixed}$ (R^2=0.35)	348	0.32	0.44 (*33*)	0.99	0.27	1.46 (*26*)	0.08
CoFSI (R^2=0.70)	95	0.65	0.17 (*31*)	1.00	0.46	1.09 (*25*)	0.40
OFSI (R^2=0.74)	95	0.68	0.24 (*27*)	0.99	0.43	1.58 (*25*)	0.11
ToFSI (R^2=0.66)	95	0.61	0.18 (*25*)	1.00	0.39	1.04 (*25*)	0.45

823

Table 2 Expected and observed relationships between traits and taxon sensitivity (↑) or tolerance (↓). (-) denotes non-significant result. Green arrows represent agreement, red disagreement and black where inconsistent results were found in the literature (†). Observed relationships taken from global literature models. See Table A1 for details of the traits and expectations included.

Category	Modality	Expected	EPSI	$EPSI_{mixed}$	CoFSI	OFSI	ToFSI
Maximum length (mm)	VSmall	↑	-	-	-	-	-
	Small	↑	↓***	-	-	-	-
	SmallMed	↓	-	-	-	-	-
	Med	↓	-	-	-	-	-
	MedLarge	↑	-	-	-	-	-
	Large	↑	-	-	-	-	-
Life cycle duration	Ephem	↓	-	-	-	-	-
	Perren	↑	↑***	-	-	-	-
Voltinism (number of generations per year)	Semivoltine	↑	-	-	-	-	↓*
	Univoltine	↑	-	-	-	-	-
	Multivoltine	↓	-	-	-	-	-
Aquatic stages	Egg	↑	↑***	↑**	-	-	-
	Larva	↑	-	-	↓*	-	↓*
	Nymph	↓	-	-	-	-	-
	Adult	↓	↓***	↓*	↓*	-	↓*
Reproduction	Oviviparity	↑	-	-	-	-	-
	Asexual	↑/↓†	-	-	-	-	-
Resistance forms	Cocoons	↑/↓†	-	-	-	-	-
Type of food	Microorganisms	↑/↓†	-	-	-	-	-
	FineDetritus	↓	-	-	-	-	-
	DeadPlant	↑/↓†	-	-	-	-	-
	Microphytes	↑/↓†	-	-	-	-	-
	Microinvs	↑	-	-	-	-	-

Feeding mode	DepsoitFeeder	↑/↓†	-	-	-	-	-
	Shredder	↑	-	↑*	-	-	-
	Scraper	↑/↓†	↑*	↑*	-	-	-
	Filterer	↑	-	-	-	-	-
Respiration	Tegument	↑/↓†	↓*	-	-	-	-
	Gill	↑/↓†	-	-	-	-	-
Mode of locomotion and relation to substrate	OpenWaterSwimmer	↑	-	-	-	-	-
	Crawler	↑/↓†	-	-	-	-	-
	Burrower	↑	↑*	↑*	-	-	-
	Interstitial	↑	-	-	↑*	-	↑*
	Attached (temporary)	↓	↑***	↑*	↑*	-	-
	Attached (permanent)	↓	-	-	-	-	-

Significance levels: ≤0.05(*); ≤0.01 (**); ≤0.001(***).

Table A1 Traits used as independent variables. Trait modes in bold indicate inclusion in the subset of traits selected from a review of the literature.

Category	**Mode**	**Short name**
Maximum length (mm)	<2.5	VSmall[1]
	2.5-5	Small[1]
	5-10	SmallMed[1]
	10-20	Med[1]
	20-40	MedLarge[1]
	40-80	Large[1]
	>80	VLarge
Life cycle duration (years)	≤1	Ephem[2]
	>1	Perren[2]
Voltinism (generations per year)	<1	Semivoltine[2]
	1	Univoltine[2]
	>1	Multivoltine[2]
Aquatic stages	Egg	Egg[3]
	Larva	Larva[3]
	Nymph	Nymph[3]
	Adult	Adult[3]
Reproduction	Ovoviviparous and care for young	Ovoviviparity[4]
	Free single eggs	IsolatedEggsFree
	Fixed single eggs	IsolatedEggsCemented
	Cemented or fixed clutches	ClutchesFixed
	Free clutches	ClutchesFree
	Endophytic clutches	ClutchesVeg
	Terrestrial clutches	ClutchesTerr
	Asexual reproduction	Asexual[5]
Dispersal	Water passive	AquaticPassive
	Water active	AquaticActive
	Areial passive	AerialPassive
	Aerial active	AerialActive
Resistance forms	Eggs, statoblasts	EggsStatoblasts
	Cocoons	Cocoons[6]
	Protection against dessication	Housing
	Diapause/dormancy	DiapauseDormancy
	None	NoResistance
Type of food	Fine sediment and microrganisms	Microorganisms[7]
	Detritus <1mm	FineDetritus[7]
	Plant detritus >1mm	DeadPlant[8]
	Living microphytes	Microphytes[9]
	Living macrophytes	Macrophytes
	Dead animals >1mm	DeadAnimal

	Living microinvertebrates	Microinvs[10]
	Living macroinvertebrates	Macroinvs
	Vertebrates	Vertebrates
Feeding mode	Absorber	Absorber
	Collector-gatherer	DepositFeeder[7]
	Shredder	Shredder[8]
	Scraper	Scraper[9]
	Filterer	Filterer[11]
	Piercer	Piercer
	Predator	Predator
	Parasite	Parasite
Respiration	Tegument	Tegument[12]
	Gills	Gill[13]
	Plastron	Plastron
	Spiracle	Spiracle
	Hydrostatic vesicle	Hydrostatic
Mode of locomotion and relationship to substrate	Flight	Flier
	Surface swimmers	SurfaceSwimmer
	Open water swimmer	OpenWaterSwimmer[14]
	Crawling	Crawler[14]
	Burrowing	Burrower[14]
	Within interstices	Interstitial[14,15]
	Attached (temporary)	AttachedTemp[14]
	Attached (permanent)	AttachedPerm[14]

[1]Small-bodied taxa more sensitive to fine sediment due to restricted dispersal in reduced pore space (Gayraud & Phillipe, 2001; Wagenhoff et al., 2012; Descloux et al., 2014). Larger taxa may also be relatively sensitive (Buendia et al., 2013)

[2]Voltinism reflects ability to recover from disturbance due to fine sediment; ephemeral and multivoltine taxa are tolerant compared to perennial and uni- and semi-voltine taxa (Buendia et al., 2013; Larsen et al., 2011)

[3]Life-stage affects ability to avoid burial (Wood et al., 2001; Jones et al., 2012)

[4]Oviviparity was less prevalent at sites impacted by colmation (Descloux et al., 2014)

[5]Prevalence of asexual reproduction exhibited a significant response to colmation but sign of relationship was inconsistent among three sites (Descloux et al., 2014)

[6]Prevalence of cocoons as a resistance form exhibited a significant response to colmation but sign of relationship was inconsistent among three sites (Descloux et al., 2014)

[7]Diets and feeding modes associated with fine sediment (e.g. Buendia et al., 2013), although effect was not consistent among three sites for fine sediment and microorganisms diet and collector-gather feeding mode (Descloux et al., 2014)

[8]Deposited sediment may limit consumption of plant detritus by shredders (Febra, 2013). Both Buendia et al. (2013) and Descloux et al. (2014) found that shredders were relatively sensitive. However, Descloux et al/ (2014) also found that the prevalence of dead plant diets increased with colmation

[9]Fine sediment may bury and dilute algal resources for scrapers (grazers) (Brookes, 1986; Suren, 2005; Kent & Stelzer, 2008; Relyea et al., 2012) yet both Buendia et al. (2013) and Descloux et al. (2014) found that scrapers were relatively tolerant of fine sediment

[10]Prevalence of living microinvertebrate diets decreased with colmation (Descloux et al., 2014)

[11]Filtering apparatus can become clogged, interrupting feeding and possibly causing abandonment (Edington & Hildrew, 1995; Strand & Merrit, 1997). Buendia et al. (2013) found that filterers were sensitive to fine sediment

[12]Prevalence of tegumental respiration decreased with colmation in three rivers (Descloux et al., 2014). However, Larsen et al. (2011) found that organisms with tegumental respiration were tolerant of sand addition.

[13]Gills can become clogged and abraded (Lemly, 1982; Jones et al., 2012). Townsend et al. (2008) and Larsen et al. (2011) both found that organisms with gills were sensitive to fine sediment. However, both Buendia et al. (2013) and Descloux et al. (2014) found that the prevalence of gills as a respiration mode increased with colmation.

[14]Locomotion traits all exhibited significant associations with fine sediment (Buendia et al., 2013; Descloux et al., 2014)

[15]Interstitial organisms are susceptible to smothering and hypoxia (Wood et al., 2005).

872 **Table A2** Results of the 'global literature' model for EPSI.
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	Estimate	**SE**	***t***	***p***
(Intercept)	0.000	0.043	0.00	1.00
VSmall	0.056	0.047	1.19	0.23
Small	-0.222	0.098	-2.27	0.02
SmallMed	-0.045	0.077	-0.59	0.55
Med	0.011	0.075	0.15	0.88
MedLarge	-0.139	0.074	-1.89	0.06
Large	0.019	0.061	0.32	0.75
Ephem	0.145	0.101	1.43	0.15
Perren	0.420	0.125	3.35	0.00
Semivoltine	-0.143	0.087	-1.65	0.10
Univoltine	-0.042	0.089	-0.47	0.64
Multivoltine	-0.065	0.105	-0.62	0.54
Egg	0.189	0.061	3.08	0.00
Larva	-0.053	0.080	-0.66	0.51
Nymph	-0.074	0.086	-0.85	0.39
Adult	-0.514	0.121	-4.26	0.00
Ovoviviparity	-0.095	0.076	-1.25	0.21
Asexual	0.062	0.052	1.17	0.24
Cocoons	-0.049	0.066	-0.73	0.46
Microorganisms	-0.025	0.056	-0.44	0.66
FineDetritus	0.058	0.088	0.66	0.51
DeadPlant	-0.099	0.076	-1.31	0.19
Microphytes	-0.089	0.069	-1.29	0.20
Microinvs	-0.116	0.072	-1.60	0.11
DepositFeeder	-0.060	0.098	-0.61	0.54
Shredder	0.170	0.088	1.94	0.05
Scraper	0.181	0.076	2.37	0.02
Filterer	-0.081	0.131	-0.61	0.54
Tegument	-0.025	0.078	-0.33	0.75
Gill	-0.065	0.077	-0.85	0.39
OpenWaterSwimmer	0.016	0.094	0.17	0.87
Crawler	0.059	0.102	0.58	0.56
Burrower	0.186	0.082	2.26	0.02
Interstitial	0.068	0.059	1.15	0.25
AttachedTemp	0.442	0.144	3.06	0.00
AttachedPerm	-0.078	0.049	-1.59	0.11

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876 **Table A3** Results of the 'global literature' model for $EPSI_{mixed}$.
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	Estimate	**SE**	***t***	***p***
(Intercept)	0.000	0.048	0.00	1.00
VSmall	0.031	0.053	0.57	0.57
Small	-0.187	0.124	-1.51	0.13
SmallMed	0.001	0.091	0.02	0.99
Med	0.014	0.094	0.15	0.88
MedLarge	-0.092	0.081	-1.13	0.26
Large	0.092	0.060	1.53	0.13
Ephem	0.067	0.117	0.58	0.57
Perren	0.086	0.137	0.63	0.53
Semivoltine	0.144	0.100	1.44	0.15
Univoltine	0.051	0.102	0.50	0.62
Multivoltine	0.118	0.113	1.04	0.30
Egg	0.174	0.066	2.64	0.01
Larva	-0.060	0.095	-0.63	0.53
Nymph	-0.007	0.092	-0.08	0.94
Adult	-0.275	0.128	-2.15	0.03
Ovoviviparity	-0.037	0.072	-0.51	0.61
Asexual	0.104	0.059	1.76	0.08
Cocoons	-0.039	0.078	-0.50	0.61
Microorganisms	-0.100	0.064	-1.56	0.12
FineDetritus	0.012	0.085	0.14	0.89
DeadPlant	-0.107	0.075	-1.44	0.15
Microphytes	-0.044	0.081	-0.54	0.59
Microinvs	-0.091	0.081	-1.12	0.26
DepositFeeder	-0.025	0.094	-0.27	0.79
Shredder	0.257	0.092	2.78	0.01
Scraper	0.243	0.089	2.74	0.01
Filterer	0.098	0.112	0.88	0.38
Tegument	-0.101	0.094	-1.07	0.29
Gill	-0.020	0.095	-0.21	0.83
OpenWaterSwimmer	0.058	0.124	0.47	0.64
Crawler	0.193	0.112	1.72	0.09
Burrower	0.154	0.074	2.07	0.04
Interstitial	0.055	0.063	0.87	0.38
AttachedTemp	0.330	0.140	2.36	0.02
AttachedPerm	-0.101	0.057	-1.76	0.08

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881 **Table A4** Results of the 'global literature' model for CoFSI.
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	Estimate	**SE**	***t***	***p***
(Intercept)	0.000	0.096	0.00	1.00
Small	-0.182	0.262	-0.69	0.49
SmallMed	-0.431	0.305	-1.41	0.16
Med	-0.056	0.237	-0.24	0.81
MedLarge	-0.356	0.270	-1.31	0.19
Large	-0.290	0.205	-1.42	0.16
Ephem	0.233	0.251	0.93	0.36
Perren	0.288	0.333	0.86	0.39
Semivoltine	-0.502	0.257	-1.95	0.06
Univoltine	-0.303	0.215	-1.41	0.16
Multivoltine	-0.322	0.262	-1.23	0.22
Egg	0.171	0.173	0.99	0.33
Larva	-0.446	0.209	-2.13	0.04
Nymph	-0.251	0.223	-1.13	0.26
Adult	-0.680	0.331	-2.06	0.04
Ovoviviparity	-0.253	0.213	-1.19	0.24
Asexual	0.201	0.175	1.15	0.25
Cocoons	0.112	0.174	0.64	0.52
Microorganisms	0.241	0.145	1.67	0.10
FineDetritus	0.170	0.240	0.71	0.48
DeadPlant	-0.182	0.165	-1.11	0.27
Microphytes	-0.166	0.195	-0.85	0.40
Microinvs	0.051	0.202	0.25	0.80
DepositFeeder	-0.226	0.259	-0.87	0.39
Shredder	0.140	0.219	0.64	0.52
Scraper	-0.238	0.250	-0.95	0.34
Filterer	-0.376	0.297	-1.27	0.21
Tegument	-0.052	0.216	-0.24	0.81
Gill	0.104	0.175	0.59	0.56
OpenWaterSwimmer	-0.038	0.170	-0.22	0.82
Crawler	0.145	0.266	0.55	0.59
Burrower	0.128	0.175	0.73	0.47
Interstitial	0.359	0.170	2.12	0.04
AttachedTemp	0.735	0.358	2.05	0.04
AttachedPerm	-0.181	0.130	-1.39	0.17

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885 **Table A5** Results of the 'global literature' model for OFSI.
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	Estimate	**SE**	***t***	***p***
(Intercept)	0.000	0.098	0.00	1.00
Small	0.014	0.268	0.05	0.96
SmallMed	-0.038	0.312	-0.12	0.90
Med	0.044	0.242	0.18	0.86
MedLarge	-0.084	0.277	-0.30	0.76
Large	0.024	0.209	0.11	0.91
Ephem	0.490	0.257	1.91	0.06
Perren	0.006	0.341	0.02	0.99
Semivoltine	0.232	0.263	0.88	0.38
Univoltine	0.183	0.220	0.83	0.41
Multivoltine	0.306	0.268	1.14	0.26
Egg	0.053	0.177	0.30	0.77
Larva	-0.064	0.214	-0.30	0.77
Nymph	-0.164	0.228	-0.72	0.48
Adult	0.110	0.338	0.33	0.75
Ovoviviparity	-0.347	0.218	-1.59	0.12
Asexual	0.025	0.179	0.14	0.89
Cocoons	-0.003	0.178	-0.02	0.99
Microorganisms	0.063	0.148	0.42	0.67
FineDetritus	-0.031	0.245	-0.13	0.90
DeadPlant	-0.291	0.169	-1.73	0.09
Microphytes	-0.136	0.199	-0.68	0.50
Microinvs	0.067	0.207	0.32	0.75
DepositFeeder	0.073	0.265	0.27	0.79
Shredder	0.143	0.224	0.64	0.53
Scraper	0.225	0.256	0.88	0.38
Filterer	-0.238	0.304	-0.78	0.44
Tegument	0.012	0.221	0.06	0.96
Gill	0.342	0.179	1.91	0.06
OpenWaterSwimmer	-0.104	0.174	-0.60	0.55
Crawler	-0.093	0.272	-0.34	0.73
Burrower	-0.079	0.179	-0.44	0.66
Interstitial	-0.084	0.174	-0.48	0.63
AttachedTemp	0.192	0.367	0.52	0.60
AttachedPerm	-0.071	0.133	-0.54	0.59

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888 **Table A6** Results of the 'global literature' model for ToFSI.
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	Estimate	**SE**	***t***	***p***
(Intercept)	0.000	0.101	0.00	1.00
Small	-0.210	0.276	-0.76	0.45
SmallMed	-0.457	0.322	-1.42	0.16
Med	-0.087	0.250	-0.35	0.73
MedLarge	-0.348	0.285	-1.22	0.23
Large	-0.335	0.216	-1.55	0.13
Ephem	-0.016	0.265	-0.06	0.95
Perren	0.316	0.351	0.90	0.37
Semivoltine	-0.689	0.271	-2.54	0.01
Univoltine	-0.440	0.227	-1.94	0.06
Multivoltine	-0.530	0.276	-1.92	0.06
Egg	0.161	0.182	0.88	0.38
Larva	-0.460	0.221	-2.08	0.04
Nymph	-0.187	0.235	-0.80	0.43
Adult	-0.818	0.349	-2.35	0.02
Ovoviviparity	-0.086	0.225	-0.38	0.70
Asexual	0.210	0.184	1.14	0.26
Cocoons	0.126	0.183	0.69	0.50
Microorganisms	0.233	0.153	1.53	0.13
FineDetritus	0.207	0.253	0.82	0.42
DeadPlant	-0.039	0.174	-0.23	0.82
Microphytes	-0.108	0.205	-0.53	0.60
Microinvs	0.020	0.213	0.09	0.93
DepositFeeder	-0.292	0.273	-1.07	0.29
Shredder	0.075	0.230	0.33	0.74
Scraper	-0.392	0.264	-1.49	0.14
Filterer	-0.285	0.313	-0.91	0.37
Tegument	-0.065	0.228	-0.29	0.78
Gill	-0.077	0.185	-0.42	0.68
OpenWaterSwimmer	0.016	0.179	0.09	0.93
Crawler	0.213	0.280	0.76	0.45
Burrower	0.186	0.185	1.01	0.32
Interstitial	0.446	0.179	2.49	0.02
AttachedTemp	0.710	0.378	1.88	0.07
AttachedPerm	-0.161	0.137	-1.17	0.25

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